

Dietary Responses to Fruit Scarcity of Wild Chimpanzees at Bossou, Guinea: Possible Implications for Ecological Importance of Tool Use

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ABSTRACT A 13-month ecological study was conducted at Bossou, Guinea, West Africa, to elucidate how a community of wild chimpanzees (*Pan troglodytes verus*) deals with the scarcity of main foods. During the study period, fruit availability fluctuated radically. The chimpanzees were confirmed to depend heavily on three "keystone resources" which were available when their main foods (fruit pulp) were scarce. These were fruits of *Musanga cecropioides*, oil-palm (*Elaeis guineensis*) nuts, and oil-palm pith. These are abundant in the chimpanzees' home range and their nutritional contents compensate for a decrease in nutritional intake from fruit pulp. The presence of these excellent backup foods may explain the high reproductive performance of Bossou chimpanzees. Here, chimpanzees consumed two of the three keystone foods using two types of tool behavior: nut-cracking for oil-palm nuts and pestle-pounding for oil-palm pith. These tool-using behaviors accounted for 31.9% of the total feeding time spent in June (the month in which the highest frequency occurred) and 10.4% in total for the year. It is suggested that the Bossou chimpanzees depend strongly on tools for their subsistence. This implies a possible function for tool technology in the evolution of our human ancestors. *Am J Phys Anthropol* 106:283-295, 1998.

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Fruit production in the tropical forest has been confirmed to be highly seasonal (e.g., Frankie et al., 1974; Sabatier, 1985; van Schaik et al., 1993), and frugivorous animals must face the season of fruit scarcity. Expansion of home ranges is a common solution to scarcity employed by migratory (e.g., birds; Karr, 1976) or wide-ranging species (e.g., orangutan; MacKinnon, 1974; Leighton and Leighton, 1983). For frugivores which have a more fixed home range, switching to less preferred foods is common (Leighton and Leighton, 1983). Such "keystone plant resources" or "keystone mutualists" have been defined as being abundant and consumed in quantities that compensate for the seasonal scarcity of the animals'

main foods (Gilbert, 1980; Terborgh, 1986). These keystone resources are thought to be crucially important for survival of the consumer community because the carrying capacity of the forest may depend heavily on these resources.

Many fig (*Ficus*) species have individually irregular fruiting patterns (Janzen, 1979) and are important keystone resources espe-

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cially in the neotropics (Terborgh, 1986). Palms are also important, producing long-lasting but protected nuts (Terborgh, 1983; Tutin et al., 1991). To exploit these keystone resources, each animal species needs species-specific adaptations (Terborgh, 1983). Therefore, niche separation among sympatric species becomes more distinct in a resource-scarce season (Gautier-Hion and Gautier, 1979; Tutin et al., 1991). Demonstration of how one species copes with fruit scarcity, in comparison with other closely related species (Wrangham, 1986) or sympatric species (Tutin et al., 1991; Yamagiwa et al., 1996; Kuroda et al., 1996), may explain the evolution of different characteristics in these species (Hladik, 1988).

Wild chimpanzees (*Pan troglodytes*) are omnivorous, but in almost all populations studied (e.g., Goodall, 1986) depend primarily on fruits. Several changes in behavior according to fruit availability have been observed. Party (or subgroup) sizes decrease when fruits are scarce (Wrangham et al., 1992) to reduce feeding competition between group members (Wrangham, 1977; Isabirye-Basuta, 1988) and male ranging area becomes smaller when food resources are scarce (Wrangham, 1977). Diet diversity tends not to correlate significantly with fruit scarcity (Tutin et al., 1991; Kuroda et al., 1996), but in Kibale, Uganda, the diversity of plant food increases when fruits are scarce (Isabirye-Basuta, 1989). With respect to dietary switches, consumption of leaves (Nishida, 1974), terrestrial herbaceous vegetation (THV) (cf. Wrangham, 1986) pith (Tutin et al., 1991; Wrangham et al., 1996), bark (Nishida, 1976), oil-palm fruit (*Elaeis guineensis*) and *Duboscia macrocarpa* fruit (Tutin et al., 1991, 1997; Kuroda et al., 1996), and fig fruit (Kuroda et al., 1996; Wrangham et al., 1996) is increased to compensate for scarcity of major fruits. Nutritional intake from animal meat obtained by hunting and from insects by tool-using behavior has been regarded as trivial in quantity (Teleki, 1973; Stanford et al., 1994).

At Bossou, Guinea, a community of wild chimpanzees (*Pan troglodytes verus*) lives in a very small and semi-isolated habitat. Their area covers only about 5 km². In addition, the forest is separated from the adjacent

Nimba Mountains by human activity (Sugiyama, 1991). Thus, Bossou chimpanzees have neither a large enough home range nor refuge outside their home range (but see Sugiyama et al., 1993; Matsuzawa and Yamakoshi, 1996). A sharp expansion of the home range appears unlikely to be an effective response to fruit scarcity for Bossou chimpanzees.

Under such conditions at Bossou, seasonal dietary change is expected to occur. The feeding repertoire of Bossou chimpanzees has been described in detail (Sugiyama and Koman, 1987, 1992). They consume a variety of vegetable foods such as the fruit pulp of many species, including figs, in addition to leaves, pith, bark, and resin among others. Consumption of animal matter has also been reported (including hunting of mammals and birds, and tool-using to acquire social insects), although it is infrequent. However, the seasonality of the proportion of these different food types is unknown.

This study aims to describe the dietary adaptations of Bossou chimpanzees to seasonal change in fruit availability, and to discuss the implications of some characteristic chimpanzee behaviors, such as tool use for their subsistence.

MATERIALS AND METHODS

Subjects

The subjects of this study were a community of wild chimpanzees at Bossou, on the southeastern edge of the Republic of Guinea, West Africa, 7°39' N and 8°30' W. A preliminary study was first conducted at Bossou in the 1960s (Albrecht and Dunnett, 1971). Since 1976, this group has been habituated to observers without provisioning, and has been studied intensively. All the individuals are well identified. Group size was 18 and no immigration or emigration was recorded during the 1995 study period. Dense foliage has made it quite difficult to observe detailed behavior of chimpanzees on the ground (e.g., nut-cracking behavior; Yamakoshi and Sugiyama, 1995). Habituation progressed rapidly just before and during this study period. The chimpanzees had become tolerant of closely located researchers (2–5 m away) even if they were on the ground in the bush,

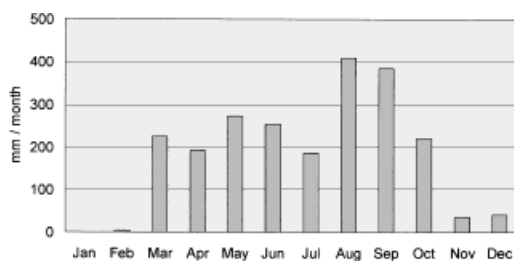


Fig. 1. Monthly rainfall at Bossou in 1995.

although most observations were done from more than 10 m away. For this reason, underestimation of behaviors occurring on the ground is becoming more negligible. In some experimental studies (for details see Matsuzawa, 1994), small amounts of fruit and/or nuts were given to the chimpanzees. In the period of this study, experimental investigation overlapped with mine for 8 days, from late January to early February in 1995. The amount of provisioned foods was reduced to a minimum (1–2 bananas/day/party).

Environment

The home range of the Bossou chimpanzees, about 15 km², including its rarely used periphery (Yokota, personal communication), is a mosaic of primary, secondary, and scrub forest, as well as farmland. Primary forest covers only about 1 km² and the most frequently used area is approximately 5 km². Surrounded by savanna vegetation, the Bossou chimpanzees' home range is separated from the large forest of the Nimba Mountains where adjacent groups of chimpanzees are known to exist (Marchesi et al., 1995). The climate is characterized by a distinct rainy season (March–October) and dry season (November–February) (Fig. 1). The monthly rainfall during the study period was measured at our field station located on the edge of the chimpanzees' core area. Total rainfall in 1995 was 2,230 mm.

Data collection

Direct behavioral observations were conducted from December 1994 to January 1996 (13 months). For simplicity, only the data in 1995 are used for the following analyses. The author used the focal animal sampling

method (Altmann, 1974). A target chimpanzee was observed for 10 min at a time, and the next target was chosen randomly from other nearby animals. This method was used to minimize disturbance from individual differences and distribute observation time evenly across animals. Infants younger than 4 years (6 animals) were excluded. The remaining 12 target animals consisted of 2 adult males, 7 adult females, 2 juvenile males, and 1 juvenile female. The name of the target animal, feeding time, species and parts eaten, diameter at breast height (DBH) of the tree eaten, and location of feeding site were recorded. Direct observation hours per month were distributed rather equally [mean hours per month: 74.5 (SD = 15.5), range: 53.6–98.4, N = 12 months, January–December 1995].

Five hundred target trees of 31 main fruit food species were selected randomly along observation routes. In principle, 20 trees for each species were selected except for rare species. Fruit availability of each tree was estimated twice a month by the author using a score of 0–4 by eye measurement. I followed the sampling design (number of target trees, sampling frequency, and sampling method) recommended by a methodological article (Chapman et al., 1994), so as to facilitate direct comparison between study sites. In addition, abundance of oil-palm nuts for nut-cracking behavior was estimated. After fruiting, the fruit bunch of the oil palm decomposes, breaks down into single nuts, and falls down to the ground. Estimates of the abundance of intact nuts scattered on the ground under each palm tree within a radius of 2 m from the base of the trunk were obtained by visual inspection, and abundance was scored over a 0–4 range.

For data analysis, I selected the 20 highest-ranking tree species (including oil-palm kernel, Table 1) a posteriori from the ranked array of annual total time spent feeding on each food item because some target species had not been consumed at all during the study period. Thus, the phenological scores of 300 trees (19 fruit species, other than oil-palm kernels) were actually used. Monthly fruit availability was represented by the sum of the number of fruiting trees (score >1) of each species in each month. A

TABLE 1. Tree species selected for fruit phenology

Species	No. samples
<i>Aningeria altissima</i>	20
<i>Antiaris africana</i>	20
<i>Canarium schweinfurthii</i>	13
<i>Celtis adolfi-frederici</i>	1
<i>Citrus aurantium</i>	20
<i>Citrus nobilis</i>	9
<i>Elaeis guineensis</i> (pulp and nut)	20
<i>Ficus</i> sp. 1	10
<i>Ficus</i> sp. 2	1
<i>Ficus</i> sp. 3	20
<i>Ficus mucoso</i>	10
<i>Ficus umbellata</i>	20
<i>Harungana madagascariensis</i>	16
<i>Mangifera indica</i>	20
<i>Morus mesozygia</i>	20
<i>Musanga cecropioides</i>	20
<i>Parkia bicolor</i>	20
<i>Pseudospondias microcarpa</i>	20
<i>Spondias mombin</i>	20
Total	300

TABLE 2. Number of items eaten and time spent feeding on them¹

Part	No. items	Feeding time (%)
Fruit pulp	80	60.7
Leaf	38	10.8
Pith (w) ²	11	10.1
Seed	1	6.3
Pith (h) ³	9	5.3
Insect	— ⁴	1.8
Flower	6	1.1
Bark	7	0.9
Root/tuber	2	0.9
Resin	2	0.6
Others	4	1.5
Total	160	100

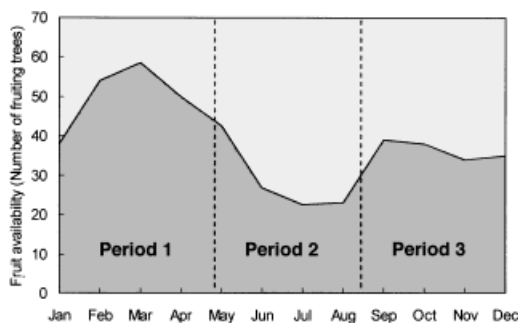
¹ No. of species = 110.² w = woody plants.³ h = herbs.⁴ Not fully identified.

Fig. 2. Seasonal change in fruit availability at Bossou in 1995. Monthly fruit availability is represented by the total number of fruiting trees out of 300 selected trees. See text for details.

monthly number is an average of 2 census days each month. As a consequence, 78.0% of the total time spent feeding on fruit pulp (47.3% of total time spent feeding) was devoted to the 19 species used in the analysis.

RESULTS

Seasonality in fruit availability

Phenological data show a strong seasonality in fruit availability at Bossou (Fig. 2). Fruits were quite abundant from the late dry season to the early rainy season (January–April: period 1). On the other hand, fruits were scarce in mid rainy season (May–August: period 2). In late rainy season and

early dry season (September–December: period 3), fruits were still scarce but more abundant than in period 2.

Diet diversity

In 1995, the chimpanzees consumed 160 items from 110 plant species (Table 2). Fruit pulp constituted 50.0% (80 items) and leaves 23.8% (38 items). Other items included were seeds (kernels), pith of woody plants (petioles and peduncles), pith of herbs, bark, flowers, resin, root, sap, dead trunk, mushrooms, and algae. In addition, 8 items from insect or products of insect (i.e., ants, bee larvae, honey, beetle larvae, gall; not yet fully identified), water, and one's own blood and feces were consumed. No vertebrates or termites were consumed during this study period, although consumption has been reported previously (Sugiyama and Koman, 1987).

As for the monthly change of food diversity (Fig. 3), there was a significant correlation between monthly fruit availability and the number of fruit items eaten (Spearman $r_s = 0.66$, $N = 12$, $P < 0.05$). However, correlation between fruit availability and the number of all items eaten was not significant [$r_s = 0.34$, $N = 12$, not significant (N.S.)]. Therefore, the chimpanzees' diet diversity did not increase when fruits were scarce.

Diet composition

During the study period, fruit pulp consumption occupied 60.7% of the total time

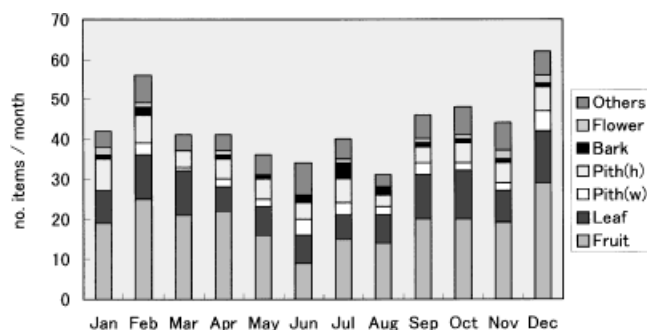


Fig. 3. Monthly diet diversity of Bossou chimpanzees in 1995. Pith (h) = herbs; Pith (w) = woody plants.

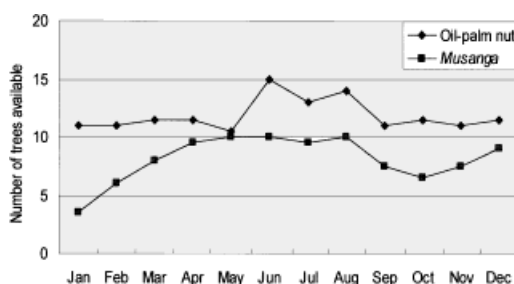


Fig. 4. Monthly change in availability of oil-palm nut and *Musanga cecropioides* fruit in 1995.

TABLE 3. Percentages of time spent feeding on each food category in each period

Food categories	Period 1	Period 2	Period 3
Fruit pulp	71.4	52.9	59.6
Fruit ¹	50.8	35.8	41.3
Fig	19.7	5.0	14.9
<i>Musanga</i>	0.9	12.1	3.4
Oil-palm kernel	0.5	8.8	8.6
By nut-cracking	0.5	8.3	8.5
Oil-palm pith	0.6	18.4	11.0
By pestle-pounding	0.1	10.4	3.9
Leaf	14.4	8.6	8.2
THV	4.3	3.1	2.7
Insect	2.1	2.0	1.9
Bark	0.1	1.7	0.9
Others	6.6	4.5	7.1
Total	100	100	100

¹ Except fig and *Musanga* fruit.

spent feeding (Table 2). In quantity, fruit pulp comprised a major part of the diet of Bossou chimpanzees. The correlation between monthly fruit availability and monthly percentages of time spent feeding on fruit pulp was highly significant (Spearman $r_s = 0.83$, $N = 12$, $P < 0.001$). Time spent feeding on fruit pulp increased when its availability increased.

Keystone resources

By definition, keystone resources should be available when main foods are scarce. For the Bossou chimpanzees, fruit pulp appeared to be the main food (Table 2). These foods were available only seasonally and were very scarce especially in period 2 (Fig. 2). What, then, did the chimpanzees eat in period 2? There are several a priori candidates for keystone resources at Bossou. From phenological data, only 2 items (*Musanga cecropioides* fruit and oil-palm nut) were available year round (Fig. 4). In addition, fig fruit, palm pith, leaf, bark, and THV have been proposed as keystone resources in other studies (see introductory remarks).

Table 3 shows the time spent feeding on each food category in each period. Fig fruits were consumed in period 2 proportionally to their availability. Fig trees displayed individual fruiting rhythms but many trees did not fruit in period 2 for unknown reasons. As a result, seasonal availability of fig fruits resembled that of total fruits. Considerable amounts of leaves were consumed, but leaf eating showed no increase in period 2 (Fig. 5; Spearman $r_s = 0.53$, $N = 12$, N.S.). Consumption of THV and insects lacked seasonality and was infrequent (correlation with fruit availability, $r_s = -0.06$, 0.55 , respectively, $N = 12$, N.S.). Consumption of bark was negatively correlated with fruit availability ($r_s = -0.59$, $N = 12$, $P < 0.05$). However, the amount of feeding time on bark was too small to make up for the large scarcity of fruits. *Musanga* fruit, oil-palm kernel, and oil-palm pith were consumed as expected. Each item was frequently eaten in period 2 (12.1%, 8.8%, and 18.4%, respectively). Feed-

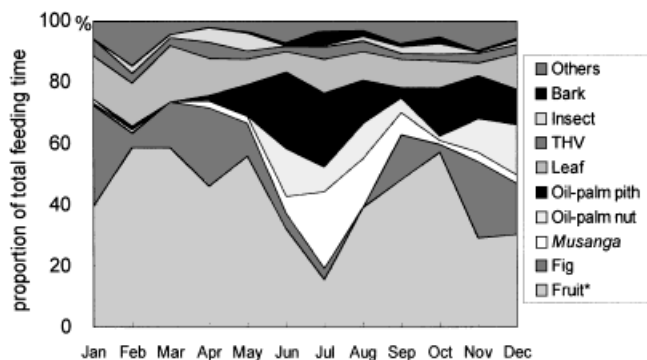


Fig. 5. Monthly change of time spent feeding on each food category by Bossou chimpanzees in 1995. *Except fig and *Musanga* fruits.

TABLE 4. Annual total time spent feeding on each food item

Species	Part ¹	%
<i>Elaeis guineensis</i>	pt	9.6
	kn	6.3
<i>Pseudospondias microcarpa</i>	fr	5.9
<i>Musanga cecropioides</i>	fr	5.3
<i>Mangifera indica</i>	fr	5.0
<i>Morus mesozygia</i>	fr	4.8
<i>Ficus</i> sp. 3	fr	3.4
<i>Citrus aurantium</i>	fr	3.1
<i>Ficus mucuso</i>	fr	2.7
<i>Ficus umbellata</i>	fr	2.6

¹ pt = pith; kn = kernel; fr = fruit pulp.

ing time on each item was negatively correlated with fruit availability (*Musanga* fruit, $r_s = -0.75$, $N = 12$, $P < 0.01$; oil-palm kernel, $r_s = -0.82$, $N = 12$, $P < 0.01$; oil-palm pith, $r_s = -0.81$, $N = 12$, $P < 0.01$). Thus, these 3 items (*Musanga* fruit, oil-palm kernel, and oil-palm pith) clearly had an important role in compensating for the general scarcity of fruits, and actually functioned as keystone resources (Fig. 5).

These 3 keystone resources ranked high among the annual sum of time spent feeding on each food item (Table 4). Oil-palm pith, kernel, and *Musanga* fruit stand first, second, and fourth, respectively. As single food items, these 3 keystone species proved to be extremely important resources.

Tool use

Several habitual tool-using behaviors have been studied at Bossou. They have focused mainly on the behavioral description of techniques involved in nut-cracking for oil-palm nuts with 2 stones as an anvil and hammer (Sugiyama and Koman, 1979), pestle-pounding for oil-palm pith with a leaf frond as a pestle (Yamakoshi and Sugiyama, 1995),

ant-dipping with wands mainly for safari ants (*Dorylus molestus*; Sugiyama, 1995a), water-drinking with chewed leaves (Sugiyama, 1995b), and algae-scooping with sticks (Matsuzawa et al., personal communication).

Tool use enabled consumption of 2 of the keystone resources. Nut-cracking behavior to obtain the inner contents occurred 97.2% of the time spent feeding on oil-palm kernels. During the remaining 2.8% of the time, oil-palm kernel contents were consumed by direct biting of the nut, without tool use.

Pestle-pounding behavior was employed in 46.5% of the time spent feeding on oil-palm pith. In a typical case of palm-pith feeding, chimpanzees first consumed much pith without tools; thereafter, pestles were used (see Yamakoshi and Sugiyama, 1995 for details). I attributed only the duration of the latter part to the feeding time involving pestle use. There were also many cases in which no tool was used throughout. Nevertheless, chimpanzees used 10.4% of their total feeding time in period 2 engaged in pestle-pounding behavior (Table 3). Moreover, there was an extremely strong negative correlation between fruit availability and feeding time on oil-palm pith with pestles ($r_s = -0.83$, $N = 12$, $P < 0.001$). There was a significant but much weaker negative correlation between fruit availability and feeding time on oil-palm pith without pestles ($r_s = -0.61$, $N = 12$, $P < 0.05$). Thus, the chimpanzees used pestles more frequently when major fruits were scarce (Fig. 6). In total, 10.4% of the annual total feeding time, 18.7% of that in period 2, and 31.9% of that in June (the month of the highest proportion) involved the use of these

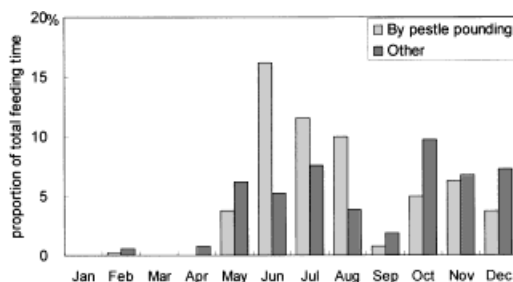


Fig. 6. Time spent feeding on oil-palm pith by Bossou chimpanzees in 1995.

2 types of tool-using behaviors (nut-cracking and pestle-pounding).

The other types of tool-using behavior were infrequent. Ant-dipping occupied 44.3% of total time engaged in feeding on insects, however, it only accounted for 0.8% of the total feeding time. Algae-scooping and water-drinking with leaves occupied 0.7% and 0.02%, respectively. Ant-dipping was observed rather aseasonally. Algae-scooping was only observed at the end of the rainy season, supposedly due to the algae's availability. The sample size of water-drinking with tools was too small to merit comment. An extremely significant negative correlation exists between fruit availability and the total time spent feeding by 5 tool-using behaviors ($r_s = -0.84$, $N = 12$, $P < 0.001$; Fig. 7). In total, these tool-using behaviors occupied 12.0% of the annual total feeding time.

As for the diurnal change in frequency of feeding, resting-grooming activity, and tool use, the following tendencies were observed (Fig. 8). Feeding activity had 2 peaks in a day. Nut-cracking peaked in the afternoon. Pestle-pounding had no clear peak. There were no special relationships between feeding, resting-grooming activity, and the frequency of occurrence of each tool use type (Spearman $r_s = 0.10$ between nut-cracking and feeding; $r_s = 0.10$ between nut-cracking and resting-grooming; $r_s = -0.13$ between pestle-pounding and feeding; $r_s = -0.09$ between pestle-pounding and resting-grooming; $N = 13$, N.S.).

DISCUSSION

Dietary shift in response to food scarcity

As in other studies in the tropical forest, there were strong seasonal fluctuations of

fruit availability for the chimpanzees at Bossou (Fig. 2). For such a semi-isolated community, ranging shifts are an unlikely solution to food scarcity. The Bossou chimpanzees apparently depend on 2 other strategies. One involves social adjustments (e.g., reducing party size; Sakura, 1994) and the other is a dietary shift to less preferred foods. The data presented here show clear evidence of a dietary shift from their main food (seasonally bearing fruits) to 3 prominent keystone plant resources (*Musanga* fruit, oil-palm kernel, and oil-palm pith) when fruits are generally scarce (Fig. 5). These 3 items appear less preferred because they are available throughout the year (Fig. 4), but are consumed only when fruit pulp is generally scarce.

The fruit of *Musanga cecropioides* was eaten during 12.1% of the total time spent feeding in period 2 when fruit pulp was generally scarce (Table 3). This species has 2 characteristics that facilitate its role as a keystone resource. First, *Musanga* trees are quite abundant in the regenerating secondary forest at Bossou. These trees are known as a leading pioneer species in West Africa (Ross, 1954; Swaine and Hall, 1983). Second, the *Musanga* fruiting pattern is unique because sometimes a single fruiting tree continues to fruit all year round. Therefore, availability of *Musanga* fruit in the study site was always high and stable (Fig. 4). Similarly, in the Kalinzu Forest Reserve, Uganda, *Musanga leo-errerae* is thought to support a high density of chimpanzees in logged areas (Hashimoto, 1995). Hence, *Musanga* may have, at least potentially, significant importance for chimpanzee subsistence.

Oil palm is no doubt an important food for chimpanzees. Its pulp is eaten in many different chimpanzee communities (McGrew, 1992). Fruit abundance of oil palm is relatively aseasonal (e.g., Wrangham, 1975). At Gombe, Tanzania, and Lopé, Gabon, oil-palm pulp is consumed by chimpanzees regardless of season (Goodall, 1986; Tutin et al., 1991) and is assumed to be a keystone resource (Tutin et al., 1997). At Bossou, there are hundreds of oil-palm trees available for chimpanzees (Kortlandt and Holzhaus, 1987). However, at least in the study

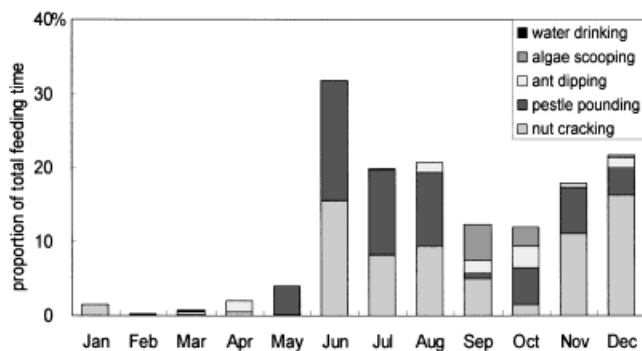
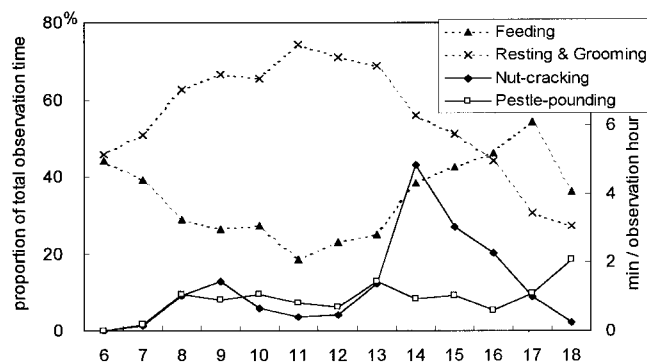


Fig. 7. Monthly change of time spent feeding using tools by Bossou chimpanzees in 1995.

Fig. 8. Diurnal rhythm of each activity by Bossou chimpanzees in 1995. Solid lines represent the observation time engaged in each tool-using behavior. Dashed lines represent proportion of total observation time engaged in each activity.



year, fruit production was very low (from the fruiting census, 1.5 of 20 target trees on average had ripe fruits; $N = 24$, $SD = 1.8$). In addition, there has always been exploitation competition with humans cutting and taking out the ripe bunches from the peripheral area of the chimpanzees' range. As a result, only 1.1% of annual total feeding time was devoted to oil-palm pulp feeding.

In contrast, oil-palm kernels were eaten in great amounts by Bossou chimpanzees (Table 4). The kernels were available throughout the year (Fig. 4), but were consumed most often when major fruit foods were scarce (Table 3, Fig. 5). As at Bossou, palm nuts were reported to play a role as keystone resources for capuchin monkeys (Terborgh, 1983; Peres, 1994). Palm nuts are potentially desirable resources for frugivorous animals as they are available for comparatively long periods and have much nutritional value (Terborgh, 1983; Hartley, 1988). However, due to their hard shells, special adaptations are necessary to consume them. For example, peccaries have strong jaws that allow them to crack the shell of palm

nuts (Kiltie, 1982). Capuchin monkeys bite open the nuts (Terborgh, 1983), and in some cases, use behavioral flexibility to bang the nuts against something hard (Izawa and Mizuno, 1977). In the case of Bossou chimpanzees, their ability with flexible tool use enables them to crack open oil-palm nuts (Sakura and Matsuzawa, 1991; Matsuzawa, 1994).

The pith of oil palm was also consumed in enormous amounts (Table 4). The pith appeared available all year round but consumption was inversely proportional to the availability of major fruit foods (Table 3, Fig. 5). Orangutans are suspected to escape to patchily distributed *Borassodendron* palms to feed on the pith when other foods are scarce (Leighton and Leighton, 1983).

These 3 food items have suitable nutritional contents to make up for the calorie loss due to overall fruit scarcity. *Musanga* fruits are rich in calories (Hladik, 1977). Oil-palm kernels are also very rich in fat and sugar (Wu Leung, 1968). Compared to almonds, an oil-palm kernel from Bossou is equivalent in fat, rich in sugar and fiber, and

poor in protein (Ota, personal communication). Nutritional analysis of oil-palm pith has not yet been done. However, in the course of pestle-pounding, the chimpanzees eat much sap after pounding deeper in the tree (Sugiyama, 1994a; Yamakoshi and Sugiyama, 1995). Oil-palm sap contains high levels of sugar (Wu Leung, 1968), so chimpanzees are able to obtain a large amount of calories.

At Bossou, both *Musanga* and oil palms are quite abundant in quantity and adequate in nutritional contents. It looks as if these 3 items completely make up for all the seasonal scarcity of other items, although they are measured only by percentage of feeding time (Fig. 5). Reproductive performance (e.g., interbirth intervals) is higher at Bossou than in other communities (Sugiyama, 1994b). Diet diversity did not increase when fruits were scarce (Fig. 3), contrary to the result that the optimal foraging theory predicts (MacArthur and Pianka, 1966). This implies that the chimpanzees do not have to feed on many different food items of low quality or high secondary compound content. They have excellent backup foods. This might also explain the absence of an increase in time feeding on leaves and THV in period 2, although this is the case at other study sites (Nishida, 1974; Tutin et al., 1991; Wrangham et al., 1996).

Fig fruits have been thought of as primarily important keystone resources (Leighton and Leighton, 1983; Terborgh, 1986; Wrangham et al., 1996; but see Gautier-Hion and Michaloud, 1989) because their fruiting pattern is aseasonal (Janzen, 1979). In this study, however, fig fruits were extremely scarce during a fruit-scarce season, so they did not serve as keystone resources (Table 3). This may have been a consequence of annual fluctuation, and further studies are needed to reach any conclusions.

Implications for ecological significance of tool use

The consumption of 2 of the 3 identified keystone foods involved 2 types of tool behavior: nut-cracking for oil-palm nuts and pestle-pounding for oil-palm pith. Both target items are firmly protected by plant organs and cannot otherwise be exploited efficiently.

The oil-palm kernel is embedded in a hard shell and is inaccessible to chimpanzees without tools. Actually, it was only in exceptional cases that chimpanzees bit open the nuts directly. Thus, no doubt, nut-cracking behavior played an indispensable role in consuming oil-palm kernels. The oil-palm pith is also hard to access as a spiny base of mature fronds surrounds it. Chimpanzees can eat the base of young shoots without tools by simply pulling out the pith. By pestle-pounding, however, the Bossou chimpanzees deepen the hole to reach the otherwise inaccessible central part of the apical bud (for details see Yamakoshi and Sugiyama, 1995) and the time spent on this tool use represented almost one half (46.5%) of the total feeding time on oil-palm pith. Pestle-pounding also played a significant role in increasing (almost doubling) the consumption of oil-palm pith.

Chimpanzees at Bossou clearly spent a significant proportion of their feeding time using tools (Fig. 7) and were likely to better exploit highly nutritional food items. In total, 10.4% of their annual total feeding time and 31.9% in June (the month of the highest proportion) involved the use of nut-cracking and pestle-pounding. Moreover, the target foods of these behaviors proved to be important keystone resources that were consumed to make up for the lack of major fruit foods at certain times of the year (Fig. 5).

In Taï forest, Côte d'Ivoire, intensive studies have revealed the fine detail of nut-cracking behavior by wild chimpanzees (e.g., Boesch and Boesch, 1983, 1984). Günther and Boesch (1993) have evaluated in detail the cost and benefit of nut-cracking behavior of Taï chimpanzees from a biomechanical approach. The chimpanzees spend approximately 2 hr and 17 min per day during the *Coula* nut season and obtain 15,752 kJ (3,762 kcal) as digestible energy, which is 9 times greater than the gross energy output. To date, a similar biomechanical study has not been done at Bossou. On the other hand, there have been few descriptions of the activity budget (e.g., percentages of time spent feeding) of Taï chimpanzees comparable with this study. Although direct comparison is impossible, it is very likely that

tool-using behaviors facilitate feeding efficiency in a similar way at both sites.

There is a clear nut-cracking season in Taï from November to March according to *Coula* nut availability (Boesch and Boesch, 1984). Fruit availability in general is supposed to be high in this season (Alexandre, 1980), in contrast to the relationship between general fruit availability and the tool-using season in Bossou (Figs. 2, 5). *Coula* nuts at Taï are a staple food resource that is consumed according to their availability. Oil-palm nuts and pith at Bossou are keystone resources that are consumed according to the availability of other food resources. Thus, the ecological significance of tool use might be different between these two sites.

Comparable ecological data have been published on termite fishing by chimpanzees in Gombe, Tanzania. There is a clear seasonal peak corresponding to the beginning of the rainy season (November) when the availability of termites becomes extremely high (Goodall, 1963; McGrew, 1992). Feeding time by termite fishing at Gombe reaches 17% of the total feeding time in November independent of the availability of other foods. However, as a yearly total, less than 5% is accounted for by termite fishing (calculated from Goodall, 1986). In the case of ant fishing at Mahale, frequency is lower and seasonality is less clear (1–2% of total observation time) (Nishida and Hiraiwa, 1982). The chimpanzees at Ndoki are reported to use a tool-set to dig out and fish for termites, enabling them to access termites found deeper in the mound (Suzuki et al., 1995). Judging from the indirect evidence, termite consumption by Ndoki chimpanzees is quite stable regardless of a seasonal fluctuation in termite activity and seems larger in quantity than that noted for other chimpanzee communities. This may be evidence for which an innovation of tool technology radically changes the chimpanzees' feeding habits, although detailed quantitative data are lacking. Hence, the percentages of time spent in tool-using at Bossou and possibly at Taï far exceed those reported for other study sites.

Nutritionally, insects are a rich source of protein but a poor source of calories for large-bodied primates (e.g., Susman, 1987). Although termites contain much protein and

fat (Hladik, 1977), insects cannot be the staple resource of nutrition. Instead, they are thought to be a dietary supplement (essential amino acid: Hladik, 1977; spice or snack: Nishida and Hiraiwa, 1982). On the other hand, oil-palm kernel and pith contain the appropriate nutritional elements (i.e., calories) necessary to compensate for a lack of staple foods. Also in this study, ant-dipping occurred quite infrequently in comparison with nut-cracking and pestle-pounding (Fig. 7). This nutritional difference in target food resources and a superabundance of oil palm at Bossou may explain the difference in dependence on tool use between nut-cracking communities such as Bossou and Taï, and other communities.

The analysis of diurnal frequency of activity supports this interpretation (Fig. 8). At Mahale, ant fishing is concentrated on during the period from noon to 4 PM and is synchronized with resting and grooming activity, not with feeding activity (Nishida, 1972). A similar pattern has also been seen at Gombe for feeding on animal matter (Teleki, 1981). Nishida (1972) supposed that ant fishing is a kind of "leisure time activity," but this was not the case for nut-cracking and pestle-pounding at Bossou (Fig. 8).

Tool use has been one of the central issues in discussions of human evolution. However, little is known about the kind of tools made before the first manufactured stone tools (e.g., Leakey, 1971). On the basis of studies of modern hunter-gatherer societies, it has been suggested that *Australopithecus* must have depended on reliable, vegetable foods such as roots, tubers, nuts, and shoots among others that were obtained by the use of a digging stick (Bartholomew and Birdsell, 1953; Tanner and Zihlman, 1976). This idea has been supported by empirical studies on the fossil bones of *Australopithecus*, which Brain et al. (1988) suggested to be digging tools, and on stable carbon isotopes from *Australopithecine* fossil teeth (Lee-Thorp et al., 1994). On the other hand, chimpanzee tool use for obtaining social insects was regarded as opportunistic and was thought to have only a trivial effect on their subsistence (Lancaster, 1968; Mann, 1972). The distinction that was made is that the tool use of chimpanzee-like apes is opportunistic

tic, while tools are indispensable for human survival (Bartholomew and Birdsell, 1953; Mann, 1972). This study clearly shows that with adequate environmental conditions, as at Bossou, wild chimpanzees do depend on tools to obtain reliable keystone resources in the critical period of the year. At least potentially, the definitions such as "man is the only mammal which is continuously dependent on tools for survival" (Bartholomew and Birdsell, 1953) and "human culture . . . a set of learned behaviours that modify the environment and are crucial to the survival of the species" (Mann, 1972) must be reconsidered.

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